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CHARACTERISTICS OF SPOTTED OWL HABITAT IN LANDSCAPES DISTURBED BY TIMBER HARVEST IN NORTHWESTERN CALIFORNIA

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ABSTRACT.—We studied Northern Spotted Owl (*Strix occidentalis caurina*) habitat characteristics within two landscapes in northwestern California. One landscape was dominated by extensive areas of previously harvested Douglas-fir (*Pseudotsuga menziesii*) forest that contained small, isolated patches of mature and old-growth forest. The other landscape was dominated by larger, less isolated patches of mature and old-growth Douglas-fir forest interspersed with previously harvested forest. Spotted Owls in the more extensively logged landscape used sites that had more complex forest structure than available sites. They also used areas that had more mature and old-growth forest than areas not occupied by owls. In the less disturbed landscape, Spotted Owls used areas that had more mature and old-growth forest than sites occupied by owls in the more disturbed landscape. Our results provide further evidence that Spotted Owls select nest and roost sites with more complex forest structure and with greater amounts of mature and old-growth coniferous forest than is generally available to them.

KEY WORDS: *Northern Spotted Owl;* Strix occidentalis caurina; *habitat selection; northwestern California; landscape; old-growth forest.*

Características del habitat de *Strix occidentalis caurina* en paisajes perturbados por la explotación de madera en el noroeste de California

RESUMEN.—Estudiamos las características del habitat de *Strix occidentalis caurina* en dos paisajes del noroeste de California. Uno de los paisajes estaba dominado por áreas de bosque (*Pseudotsuga menziesii*) que habían sido intensamente explotadas y que contenían pequeños parches de bosques maduros. El otro paisaje estaba dominado por parches mas grandes y menos aislados de bosques maduros y bosques de *Pseudotsuga menziesii* con espacios entre sí de bosques explotados. *Strix occidentalis caurina* en los paisajes extensivamente explotados utilizó los sitios que poseían estructuras de bosque mas complejas, así mismo, usó mas las áreas con bosques maduros que las áreas no ocupadas por buhos. En el paisaje menos perturbado *Strix occidentalis caurina* utilizó mas las áreas con bosques maduros que las que estaban ocupadas por buhos en paisajes mas perturbados. Nuestros resultados proveen evidencias de que *Strix occidentalis caurina* prefiere sitios para sus nidos y perchas en bosques con estructuras mas complejas y con mayores extensiones de bosques maduros y de coníferas de las que generalmente hay disponibles para ellos.

[Traducción de César Márquez]

The Northern Spotted Owl (*Strix occidentalis caurina*) usually inhabits mature and/or old-growth conifer forests (see review in Gutiérrez et al. 1995). However, they sometimes occur in habitats disturbed by either logging or fire (Forsman et al. 1977, Folliard et al. 1993). The ecological and management significance of Spotted Owls occupying disturbed forests are not fully understood (Thomas et al. 1990). Because of the political controversy surrounding this owl (Gutiérrez et al. 1996), observations of Spotted Owls occupying disturbed habitat are used as evidence that they are adaptable to habitat perturbation (e.g., Easterbrook 1994). This is particularly true of coastal northwestern California where many owls occupy disturbed redwood (*Sequoia sempervirens*) and Douglas-fir (*Pseudotsuga menziesii*)/redwood forests. The high density of owls in coastal redwood forest

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Table 1. Habitat composition of areas extensively disturbed by logging (Arcata Resource Area [ARA]) and areas less disturbed by logging (Willow Creek Study Area [WCSA]) in northwestern California.

	Percentage of Area in Each Habitat Type				
Study Areas	Water	Herb/Brush[a]	Pole/Medium	Mature/Old-growth	Hardwood
ARA	<0.01	49.2	9.4	19.8	21.6
WCSA	0.3	23.3	12.8	35.3	28.3

[a] Amounts of herbaceous and brush were combined because separate amounts of these habitat types were not available for the entire ARA.

motivated a delisting proposal for the threatened Northern Spotted Owl by the timber industry for all of northern California (see USDI 1994).

Previous studies suggest that Northern Spotted Owls are habitat specialists and they select habitats differentially (Noon and McKelvey 1996) at the microhabitat (LaHaye 1988, Solis and Gutiérrez 1990), home range (Forsman et al. 1984, Solis and Gutiérrez 1990), and landscape levels (Ripple et al. 1991, Carey et al. 1992, Johnson 1993, Lehmkuhl and Raphael 1993, Hunter et al. 1995). Studies of nesting owls in disturbed redwood forests support this pattern; habitat use is influenced by the amount of older forest and/or the presence of remnant older trees (Folliard et al. 1993).

In this paper we examine patterns of habitat use by Northern Spotted Owls at both the microhabitat and landscape scales in Douglas-fir forests disturbed by extensive past timber harvest. We first assess the structure of habitats used by a subpopulation (*sensu* Wells and Richmond 1995) of Spotted Owls in an area where old forest remained as small, isolated patches within a matrix of previously logged forest. We then compare the spatial patterns of habitat use of this subpopulation to that of a subpopulation using areas where the remaining old forest occurred as larger, less isolated patches. In this way, we strive to shift the debate of owl use of logging-disturbed forests from a political (e.g., Easterbrook 1994) to a scientific one.

STUDY AREA AND METHODS

The subpopulation of Spotted Owls in the more disturbed landscape was in the Arcata Resource Area (ARA). The ARA is administered by the U.S. Department of the Interior, Bureau of Land Management, and consists of areas ranging in size from 60–2610 ha scattered throughout northwestern California. Areas within the ARA vary with respect to the degree of their disturbance. Most are surrounded by large tracts of previously logged forests. Prior logging was often partial harvest but clear felling has also occurred extensively. Previously harvested areas are typically dominated by various age-classes of tanoak (*Lithocarpus densiflora*) and other hardwoods. Undisturbed areas have an overstory of Douglas-fir with a midstory comprised of tanoak, madrone (*Arbutus menziesii*), canyon live oak (*Quercus chrysolepis*), and other hardwoods. Other areas have oak woodlands, grasslands, and natural brushlands. The topography is steep and mountainous. Climate is Mediterranean with cool, wet winters and warm, dry summers. See Chávez-León (1989) for more information on the ARA. Some areas of the ARA were not surveyed for Spotted Owls because they contained unsuitable habitat, either grassland, brushland, or they are composed of very young forests (<20-yr old). In total, 44 areas were thoroughly surveyed for Spotted Owls between 1988–92.

The less disturbed landscape was in the 292 km^2 Willow Creek Study Area (WCSA) and consisted of lands administered primarily by the U.S. Department of Agriculture, Forest Service. Much of the WCSA consists of mature and old-growth Douglas-fir forest, but the size and connectivity of these older stands is quite variable. The primary logging disturbance on the WCSA has been clear felling of small (usually <50 ha) areas of contiguous forest. Previously harvested areas consist of various age classes of younger Douglas-fir and tanoak trees. Overall, the WCSA has more old forest than the ARA (Table 1) The floristics, topography, and climate of the WCSA are similar to the ARA. Hunter et al. (1995) provided more information on the WCSA. The WCSA has been the site of a long-term Spotted Owl demographic study (Franklin et al. 1996b), but for this study we only used owl data collected from 1988–92.

Owl Surveys. We surveyed both study areas during the breeding season using standard methods (Franklin et al. 1996a). We conducted nighttime surveys using vocal imitations of owls. After we detected owls at night, we located and mapped their roost locations during the day We fed roosting owls live mice (*Mus musculus*) and followed them to nest sites and/or young if present. We conducted at least two (and as many as nine) well-spaced night surveys and/or daytime follow-up surveys during each breeding season at each known or potential owl territory. We assigned individuals or pairs of owls to a specific territory when we located them in the same area at least twice. At WCSA, all owls were banded (see Franklin et al. 1996b).

Habitat Structure. In the ARA, we measured microhabitat characteristics within forest stands used by nesting or roosting Spotted Owls. For comparison, we measured available habitats at random locations outside of nest or

Table 2. Comparison of habitat types used to map the Arcata Resource Area (ARA) and the Willow Creek Study Area (WCSA), northwestern California.

HABITAT TYPE	ARA	WCSA
Herbaceous	<25% canopy closure (CC), all woody plants <2.5 cm diameter at breast height (DBH).	<30% CC, >50% of ground cover comprised of forbs, grass, rock, soil, and woody plants <2.5 cm DBH.
Brush	<25% CC, any woody plants 2.5–15.2 cm DBH.	<30% CC, >50% of ground cover comprised of brush, conifer, and hardwood species 2.5–12.6 cm DBH.
Pole and medium conifer	>25% CC, >50% of overstory dominated by 15.2–61.0 cm DBH conifers.	≥30% CC, >50% of conifer basal area comprised of trees ranging from 12.7–53.2 cm DBH.
Mature and old-growth	>25% CC, >50% of overstory dominated by conifers ≥61.0 cm DBH.	≥30% CC, >50% of conifer basal area comprised of trees ≥53.3 cm DBH.
Hardwood	>25% CC, overstory dominated by hardwoods >15.2 cm DBH.	≥30% CC, >80% of basal area comprised of hardwood trees >12.6 cm DBH.

roost stands. We first delineated Spotted Owl nest or roost stands using aerial photographs (scale 1:12 000) as the sum of all contiguous mature/old-growth forest (including previously-logged forest if residual old trees remained) adjacent to roosts and nests. We then established plots at five random locations within every nest and roost stand to estimate used habitat characteristics. In order to adequately sample habitat variation within larger nest and roost stands, we randomly located one additional plot for each 20-ha increase in stand area. Outside of nest and roost stands we established one plot at a random distance along each of eight 1500-m lines (approximating the radius of an owl home range) extending outward from the edge of each nest or roost stand. All random plots were located in forests. These lines extended from each stand to the north, northeast, east, southeast, south, southwest, west, and northwest. Data were combined for all used and available plots at each owl site such that each site was represented by a single average owl sample and a single average random sample.

We measured 67 microhabitat variables at plots following procedures described by Solis (1983), LaHaye (1988), and Chávez-León (1989). At each plot, we used a 20 basal area factor Bitterlich angle to determine which trees would be included in each variable radius plot (Dilworth 1981:259). For each tree in the plot we recorded species, diameter at breast height (DBH), and growth condition. We recorded the height of four trees in every one of the five DBH class intervals: 10.1–12.4, 12.5–27.4, 27.5–52.4, 52.5–89.9, and ≥90 cm.). We estimated canopy closure at plot center by averaging four readings of a spherical densiometer. We measured ground cover along a 22.6 m line oriented north-south, and centered at the middle of each sample plot; the length of the line intercept represented the diameter of a 0.04 ha circular plot. We measured the intercept of trees ≤10 cm in DBH, shrubs, herbs, litter, and coarse woody debris along this line.

We reduced 67 potential variables for analysis by first eliminating those variables that potentially would not occur on all plots. We then examined all possible correlations among variables and eliminated one member of a pair of highly correlated variables, retaining the one that was most biologically interpretable. We included some variables in the final *a priori* selection that have been used to characterize Spotted Owl habitat in other studies even though it may have been correlated with another habitat variable.

We then conducted a two-group multivariate analysis of variance (MANOVA, Dixon et al. 1990) using the 10 microhabitat variables resulting from the above filtering process. We used Hotelling-Lawley Trace to test the significance of the MANOVA. Following a significant MANOVA, we used *post-hoc* *t*-tests to test for differences in individual variables between owl and random plots (Stevens 1986:122–125).

Landscape Structure. We mapped habitat within the ARA using interpretation of 1:12 000 color aerial photographs from 1988 and 1992. We used the Wildlife Habitat Relationships system (Mayer and Laudenslayer 1988) to describe habitat types. We characterized habitat types by successional stage of coniferous forest or other broad vegetation type (Table 2). We estimated the proportion of each habitat type within the ARA by measuring habitat type polygons on 1:24 000 topographic maps using a planimeter after the boundaries of habitat types were transferred from the air photos to topographic maps.

We mapped habitat types within the WCSA using 1990 Landsat Thematic Mapper (TM) digital imagery. Hunter et al. (1995) provided detailed information on the methods used to map and assess the accuracy of habitat classifications within the WCSA. Successional stages were classified according to the criteria listed in Table 2. Given the spatial resolution (625-m^2 grid-cells) of Landsat TM data, we were unable to map most areas of water. We estimated amounts of habitat types using the IDRISI geographic information system (Eastman 1992).

We used two different methods for spatial habitat assessments because we did not have access to Landsat imagery for the ARA. In order to test that the two methods

Table 3. Spotted Owl habitat characteristics within used and available habitats in the Arcata Resource Area, northwestern California.

Variable	Used Habitats ($N = 14$)		Available Habitats ($N = 11$)				
	Mean	SE	Mean	SE	t	df[a]	P-Value[b]
Live tree basal area (m^2/ha)	221.70	46.47	184.53	11.78	2.77	16	0.014
Conifer basal area (m^2/ha)	102.80	14.87	79.28	17.74	1.02	21	0.321
Hardwood basal area (m^2/ha)	118.57	13.06	105.25	11.32	0.77	23	0.449
Snag basal area (m^2/ha)	12.60	1.98	10.58	2.34	0.66	21	0.518
Tree cover (%) (<10 cm DBH)	4.01	0.81	9.35	3.71	−1.40	11	0.188
Woody debris (%)[c]	1.80	1.05	0.61	0.25	1.10	14	0.288
Canopy closure (%)	94.82	0.89	85.45	3.09	2.91	12	0.013
Mean DBH (cm)	66.72	5.05	51.01	3.72	2.50	22	0.020
Variance of DBH	1040.58	142.62	536.84	103.22	2.86	22	0.009
Mean height (m)	82.25	4.44	65.69	6.03	2.21	19	0.039

[a] *t*-tests were for unequal (separate) variances. Thus, degrees of freedom were approximated and may vary among different variables (see Dixon et al. 1990).

[b] Results are from univariate *post-hoc t*-tests. A two group MANOVA (Zar 1984) also resulted in significant differences between habitat characteristics in stands used by owls and available stands ($F = 5.28$, df = 10,14, $P = 0.002$).

[c] Woody debris is coarse debris with the large end diameter greater than 30 cm.

of habitat assessment did not influence the outcome of the between study area comparison, we randomly selected eight (25% of the sample) WCSA owl territories from among those we used in the between study comparisons. We then classified habitats on those eight territories using air photos. Finally, we compared the Landsat classification with the air photo classification. In no case did we find significant differences in the area of the habitat types estimated using the different methods. For example, for the key variable of mature/old-growth forest area we estimated an average of 107.72 ha (SE = 10.05) and 100.23 ha (SE = 11.72) within 800 m circles using air photos and Landsat TM data, respectively ($t = 0.2354$; $P = 0.818$). Since the habitat classes we compared were broad, the two methods were likely to produce similar classifications. Consequently, we felt it was justified to use the results of the different methods in the analysis.

We measured all landscape variables within 800 m (200 ha) circular plots around owl locations on the ARA and WCSA. We chose this plot size because it represented one-half the mean nearest-neighbor distance (1579 m) between 1990 Spotted Owl territory centers at WCSA (Hunter et al. 1995), and, therefore, represented an ecologically derived plot. This plot size also reduced overlap between adjacent plots. If a nest was located for a particular territory, the corresponding plot was centered on that nest. If only a roost was located for a particular territory, the corresponding plot was centered on that roost. If more than one nest or roost was detected for a territory, one location was randomly chosen from among those available. We selected a random subset of nest and roost locations from the available WCSA owl locations that was equal to the total number of nest and roost locations found in the ARA. Within the ARA, we located 800-m circular plots at the geometric center of random areas that were not occupied by owls. We measured the proportion of each habitat type within each 800-m circular plot and used these proportions to calculate Simpson's (1949) heterogeneity index, which was a measure of the heterogeneity of successional stage vegetation. We compared landscape characteristics around owl sites in the ARA and the WCSA with Mann-Whitney (MW) tests (Zar 1984). We also compared landscape characteristics at used and unused areas in the ARA with MW tests.

RESULTS

We found 29 owl territories in 44 separate areas (66%) within the ARA and 50 territories within the WCSA. In the ARA, we sampled microhabitat in 14 Spotted Owl nest or roost stands; random plots were located around 11 of these stands to estimate available habitat characteristics. We did not establish random plots at all occupied areas due to lack of access to adjacent private lands. Therefore, we only sampled microhabitat characteristics in the 14 stands because we could not achieve reasonably equal samples of used and available habitats.

We used 10 of the microhabitat variables measured for the two-group MANOVA (Table 3). Hotelling-Lawley Trace indicated there was a significant difference between the characteristics of habitats used by owls and those available (Test Value = 3.77, $F = 5.28$, df = 10,14, $P = 0.002$). Habitats used by owls had higher values for all 10 habitat features except for small tree cover, indicating that owls used habitats characterized by greater structural diversity. The higher mean value for small tree cover in available habitats probably reflected

Table 4. Landscape characteristics within 800 m radius (200 ha) plots around Spotted Owl sites at the Arcata Resource Area (ARA) and the Willow Creek Study Area (WCSA), northwestern California.

	ARA (N = 29)		WCSA (N = 29)			
VARIABLE	MEAN	SD	MEAN	SD	z[a]	P-VALUE
Habitat type (%)						
Herbaceous	6.1	6.2	4.2	3.0	0.40	0.692
Brush	24.4	19.2	9.7	8.6	3.06	0.002
Pole and medium conifer	7.1	13.0	14.1	6.3	4.08	<0.001
Mature and old-growth	31.8	20.3	49.6	14.0	3.17	0.002
Hardwood	30.5	20.4	22.4	8.2	1.73	0.083
Landscape index						
Habitat heterogeneity[b]	0.6	0.1	0.6	0.1	1.56	0.118

[a] Mann-Whitney test statistic (Zar 1984).
[b] Estimated using Simpson's (1949) index.

conifer regeneration and/or hardwood establishment following logging. Five vegetation features were significantly different between used and available habitats (Table 3).

Of the occupied areas on the ARA, landscape plots were centered on nine nest locations and 20 daytime roost locations. For comparison of landscape characteristics, we centered landscape plots on nine nest sites and 20 roost sites randomly selected from the 50 territories on the WCSA. Owl sites at WCSA had less brush and hardwood, more pole/medium-sized conifer, and more mature/old-growth than did owl sites at ARA but amounts of herbaceous habitat types and habitat heterogeneity were not different between ARA and WCSA (Table 4).

Sites used by Spotted Owls at ARA had less brush, more mature and old-growth, and lower habitat heterogeneity than unused sites (Table 5). Amounts of herbaceous, pole/medium-sized conifer, hardwood, and habitat heterogeneity were not different between used and unused sites at ARA although hardwood comprised 10% more of the area at used sites.

DISCUSSION

Previous studies at the WCSA (LaHaye 1988, Solis and Gutiérrez 1990, Hunter et al. 1995) and in coastal redwood forest (Folliard et al. 1993) showed that owls used habitats with greater amounts of mature and old-growth forest and more complex forest structure than available sites. Within both landscapes we studied, sites used by owls had more mature/old-growth forest than

Table 5. Landscape characteristics within 800 m radius plots (200 ha) within areas used and unused by Spotted Owls at the Arcata Resource Area, northwestern California.

	USED AREAS (N = 29)		UNUSED AREAS (N = 15)			
VARIABLE	MEAN	SD	MEAN	SD	z[a]	P-VALUE
Habitat type (%)						
Herbaceous	6.1	6.2	6.3	8.8	0.68	0.496
Brush	24.4	3.7	40.0	17.6	2.71	0.007
Pole/medium conifer	7.1	13.0	10.8	12.6	1.45	0.148
Mature/old-growth	31.8	20.3	22.2	11.4	1.67	0.095
Hardwood	30.5	20.4	20.7	15.1	1.51	0.131
Landscape index						
Habitat heterogeneity	0.60	0.09	0.65	0.11	1.82	0.07

[a] Mann-Whitney test statistic (Zar 1984).

available sites, suggesting that owls select sites with more older forest. While owls established territories with comparatively low amounts of old forest on the more disturbed landscape, it was not clear if this influenced owl fitness. However, Chávez-León (1989) found that the number of young fledged per owl pair during a 2-yr (1987–88) period was significantly lower on the ARA ($\bar{x}$ = 0.47) than on the WCSA ($\bar{x}$ = 0.65; t = 5.61, df = 135, $P < 0.001$). We were unable to expand this comparison because survey effort subsequent to 1988 was different between the two areas.

Our results indicate that owls select habitats differentially within their territories at both microhabitat and landscape scales. While the amount and condition of older forest stands was important, the presence of younger stands or brush stands, which also provide habitat for owl prey, could potentially offset the influence of reduced amounts of nesting and roosting habitat (Zabel et al. 1993, Hunter et al. 1995, Franklin 1997). However, the difference in the amount of brush between used and unused areas within the ARA suggests that at some point the amount of brush may have a negative influence on site occupancy by Spotted Owls. Had our surveys at the ARA included areas we classified as unsuitable for Spotted Owls due to the absence of mature and old-growth forest, the differences we observed in the amounts of brush between used and unused areas would have been even more pronounced. Spotted Owl fragmentation threshold tolerances also have been suggested in both field (Johnson 1993) and theoretical studies (Lande 1987).

Some redwood forests harvested for timber have high densities of Spotted Owls (Thomas et al. 1990). These areas are promoted as evidence of the adaptability of Spotted Owls to logging disturbance not only in redwood forests but other forests as well (USDI 1994). Because redwood forests constitute <7% of the range of the Northern Spotted Owl (Thomas et al. 1990), have different climates and productivity, and a third of our survey sites in Douglas-fir forests did not support owls, land managers and policy makers should use caution in applying results from owl studies in logging-disturbed redwood forests to the much larger Douglas-fir region inhabited by Northern Spotted Owls.

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